RHODORA, Vol. 100, No. 903, pp. 239–260, 1998

DISTRIBUTION OF *DROSERA FILIFORMIS* AND *D. TRACYI* (DROSERACEAE): PHYTOGEOGRAPHIC IMPLICATIONS

BRUCE A. SORRIE

160 West Rhode Island Ave.,
Southern Pines, NC 28387

ABSTRACT. *Drosera filiformis* and *D. tracyi* occupy allopatric ranges, except for one restricted area in northwest Florida. *Drosera filiformis* is nearly restricted to the Atlantic Coastal Plain; *D. tracyi* is restricted to the Gulf Coastal Plain. The two species have been found to grow sympatrically in only one limited area. Natural hybrids are unknown. The distribution of *D. filiformis* is notable for its series of disjunct populations; only three other Atlantic Coastal Plain species are distributed in a similar pattern. The distribution of *D. tracyi* is continuous and without disjunctions. Many Gulf Coastal Plain species share this pattern, including close relatives of the four Atlantic disjuncts. It is postulated that the Atlantic disjuncts assumed their current discontinuous distributions through a series of short to moderately long dispersal events, followed by a loss of intervening populations. Either the Atlantic disjuncts were derived from their Gulf Coast counterparts, or both geographic groups were derived from a now extinct precursor.

Key Words: Atlantic Coastal Plain, Gulf Coastal Plain, distribution, disjunct, seepage bog, freshwater pond, Pleistocene, species pair, phytogeographic pattern

The "thread-leaved sundews" or "dew-threads" of the Atlantic and Gulf Coastal Plains have been variously treated by authors as two species, as varieties of *Drosera filiformis*, or as synonyms. *Drosera filiformis* Raf. was described early in the nineteenth century (Rafinesque 1808) and *D. tracyi* Macfarlane ex L. H. Bailey early in the twentieth (Bailey 1914). Authors who recognize them as distinct species include Clewell (1985), Godfrey and Wooten (1981), Shinners (1962), Small (1933), and Wilhelm and Burkhalter (1994). Authors opting for varietal status include Fernald (1931, 1950), Harper (1914), Kartesz (1994), Murry and Urbatsch (1979), Schnell (1976), Wood (1960), and Wynne (1944). Authors treating them as synonyms include Gleason and Cronquist (1991), Jones and Coile (1988), Lowe (1921), MacRoberts (1989), and Radford et al. (1968). Prior to Macfarlane's description of *D. tracyi* in 1914, authors used the name *D. filiformis* for plants throughout the combined range of the taxa.

I consider these two sundews to be distinct species. In the past, incomplete or inaccurate morphological descriptions and conflicting statements of range in many of the above-cited publications have obscured the distinctiveness of these species. In the Results section I present evidence to support my contention.

In this paper, the geographical ranges of *Drosera filiformis* and *D. tracyi* are examined for phytogeographic patterns, how these patterns might have evolved, and what these patterns might indicate about the origin and taxonomy of these species.

MATERIALS AND METHODS

Data on the distribution of *Drosera filiformis*, *D. tracyi*, and others discussed in this paper were obtained from direct field observations, herbarium specimens, Natural Heritage Program databases, and literature reports. Field observations were made during the past twenty-five years in nearly every state in the U.S. and the Canadian province in which these species occur. Herbarium records were obtained during visits to A, CONN, DUKE, FLAS, FSU, GA, GH, IBE, LSU, MASS, MISSA, NCSC, NEBC, NLU, NMMA, NCU, PH, USA, USCH, VDB, and VSC. Data from specimen labels are written as the collector stated. State Natural Heritage Programs have provided specimen, locality, and habitat data for critical records. Several important records came from the taxonomic and floristic literature and are cited under Distribution in the Results section.

Statistical data on species endemic to the Gulf Coastal Plain are my own, based on literature and herbarium studies.

Identification of *Drosera* specimens is based on the keys provided by Godfrey and Wooten (1981) and Shinners (1962), with corrections (see Results section). Measurements were obtained with a millimeter rule from a minimum sample of twenty-five specimens of each species.

Data on phenology and habitat were obtained from specimen labels, by direct observations of both species, and from knowledgeable botanists.

For convenience, nomenclature of taxa in this paper follows that of Kartesz (1994), except for *Drosera tracyi*, which he treats as *D. filiformis* Raf. var. *tracyi* (Macfarlane) Diels, and *Sabatia foliosa*, which he treats as *S. dodecandra* (L.) BSP. var. *foliosa* (Fern.) Wilbur.

Table 1. Comparison of selected characters of *Drosera filiformis* and *D. tracyi.*

Character	*D. filiformis*	*D. tracyi*
Leaf length	8–25 (−30) cm	30–50 cm
Scape length	6–26 cm	25–60 cm
Petal length	7–10 (−12) mm	12–17 (−20) mm
Color of glandular hairs	red to dark red	pale green
Color of dried specimen	dark red to dark brown	pale greenish brown
Color of living plant in transmitted light	reddish	white

RESULTS

Taxonomic rank of the taxa. In this section I present data that support my view that *Drosera filiformis* and *D. tracyi* are distinct species. Table 1 compares selected characters, based on herbarium specimens. These data include several corrections to keys and descriptions in the literature. For example, Small (1933) states that *D. tracyi* ranges from 3–6 cm tall, rather than 3–6 dm, apparently a typographical error. Plants of *D. filiformis* typically range from 0.8 to 2.6 dm in height. To botanists familiar with *D. filiformis* in the field, encountering a population of *D. tracyi* with leaves and scapes half a meter tall is an arresting sight. Godfrey and Wooten (1981) state that the flowering scape of *D. tracyi* has green, glandular trichomes, when in fact scapes of both species are glabrous; only the leaves bear glandular hairs. Wynne (1944) states that the petal length of *D. filiformis* is 7–15 mm and that of *D. tracyi* is 12–15 mm. Actually, petals of *D. filiformis* range from 7–10 mm (rarely to 12 mm); those of *D. tracyi* range from 12–17 mm long, with exceptionally large specimens reaching 20 mm. Petals of both species are erose along the outer margin (contra Schnell 1976). Both species may produce up to 24 flowers per raceme (contra Wynne 1944, and Godfrey and Wooten 1981), although the norm is a third to half as many (pers. obs.). With appropriate corrections in place, the keys and descriptions in Godfrey and Wooten (1981), Wynne (1944), and Schnell (1976) easily distinguish the two species.

All specimens and living plants of *Drosera filiformis* that I have seen exhibit relatively short stature, thin leaves and scapes, red glandular hairs, small flowers, and small fruits. By comparison, *D. tracyi* is robust and roughly twice as tall, with thick leaves and scapes, pale green glandular hairs, large flowers, and large fruits. An additional field character is the hue of the leaves, especially when backlit. In both species the glands produce a translucent effect, but plants of *D. filiformis* are red tinged, whereas those of *D. tracyi* are strikingly white. Photographs in Schnell (1976) show this character fairly well.

In addition to morphology, these species are phenologically and ecologically separated. Data from herbaria and my own field work indicate a blooming period from mid-April to early June for *Drosera tracyi*. *Drosera filiformis* flowers from late May to September, depending on water level (in general, onset of flowering is later with increasing latitude). Thus, there appears to be only a brief span of time in late May to early June in which the two species might hybridize. The habitat of *D. filiformis* is primarily exposed shores of freshwater ponds and lakes, but also streamside seepage bogs (New Jersey), interdune swales, coastal peat bogs (Nova Scotia), roadside depressions, and borrow pits (scrapes and depressions where sand has been extracted for road building or other uses). In contrast, *D. tracyi* occupies gently sloping seepage bogs (the term "hillside bog" is often used in the South) and ecotones between pine savannas and bay-gum-cypress wetlands. It rarely inhabits shores of sinkhole ponds (= limesinks, ponds formed in solution depressions in limestone bedrock). The bog and ecotone habitats of *D. tracyi* are maintained by recurring fires (generally 2–5 year intervals); habitats of *D. filiformis* seldom burn, except New Jersey seepage bogs and the North Carolina savannas and bays. Although the pitcher plant habitats occupied by *D. tracyi* have traditionally been called "bogs" (Folkerts 1991), they are neither peatlands nor true ombrotrophic bogs. Habitat moisture is derived primarily from acidic seepage water forced to the surface by underlying clay soils; therefore these communities are better termed oligotrophic fens or poor fens.

Finally, intermediate character states, whether in living plants or herbarium specimens, have yet to be documented. Mensural characters of the two species may overlap slightly (Table 1), but the great majority of specimens examined do not approach those values. Anderson (1991) found a site in Washington County, Florida, where the two species occurred together, with "no signs of intergradation."

Figure 1. Distribution of *Drosera filiformis* and *D. tracyi.* Solid dots = *D. filiformis* (Nova Scotia to Florida); open circles = *D. tracyi* (Georgia to Louisiana). Note that both species occur in Bay and Washington Counties, Florida.

Distribution—*Drosera filiformis.* Figure 1 maps the distribution by county and province of *Drosera filiformis* and *D. tracyi* in the U.S. and Canada. The distribution of *D. filiformis* is composed of disjunct areas of occurrence. Except for a small area in the panhandle of Florida, *D. filiformis* occurs entirely on the Atlantic Coastal Plain.

Botanists have long known that *Drosera filiformis* occurs in the pine barrens region of Massachusetts, Long Island (New York), and New Jersey; these locations are well represented by specimens in regional and national herbaria. However, documentation of its occurrence elsewhere is poorly known, in part because these data have not been incorporated into regional manuals or monographic treatments, such as Fernald (1950), Gleason and Cronquist (1991), Shinners (1962), Wood (1960), and Wynne (1944).

In Rhode Island, a dozen *Drosera filiformis* plants were found in 1977 in a moist borrow pit near Worden's Pond in South Kingstown, Washington County (Tucker 1978). Associates included *Vaccinium macrocarpon* Aiton, *Lycopodiella inundata* (L.) Holub, and *Rhexia virginica* L.; *Tucker s.n.* (NEBC). *Drosera filiformis* was extant as of 1990, but the site is slowly succeeding to woody vegetation (R. Enser, Rhode Island Natural Heritage Program, pers. comm.). It is odd that more populations have not been found, since southern Washington County supports excellent quality pitch pine barrens, including a number of kettlehole ponds, which would seem to offer suitable habitat.

In Connecticut, *Drosera filiformis* was discovered in 1963 (Link 1965). Some 75 plants occurred in a moist borrow pit along Latimer Brook in East Lyme, New London County; *Link s.n.* (CONN). Associated species included *Vaccinium macrocarpon* Aiton, *Kalmia angustifolia* L., *Rubus hispidus* L., *Drosera intermedia* Hayne, *Iris prismatica* Pursh ex Ker-Gawler, and *Calopogon tuberosus* (L.) BSP. L. J. Mehrhoff (University of Connecticut herbarium, pers. comm.) states that this population was last seen about 1986 and that the site has become overgrown and much drier. Link (1965) also relates the discovery of a specimen of *D. filiformis* in the herbarium of the Connecticut Botanical Society from South Glastonbury, Hartford County. I have been unable to verify this record. South Glastonbury lies in a region of glacial outwash supporting coastal plain plants, and so the report is certainly plausible. It is likely that the populations in Connecticut and Rhode Island originated from propagules that invaded early successional habitats, and that these are short-lived populations. A likely source of propagules is Suffolk County, New York, where *D. filiformis* is abundant and which lies in the direction of prevailing winds.

In Delaware, Fernald (1931) mapped *Drosera filiformis* in Sussex County, but neither Tatnall (1946) nor I was able to find a voucher and the Delaware Natural Heritage Program has no verified record of its occurrence (K. Clancy, pers. comm.).

In Maryland, there are two vouchered locations. Charles County: bog adjacent to artificial lake in Cedarville State Forest, 1 Jul 1972, *Lee and Norden s.n.* (NY). This record was reported by Lee and Norden (1972). Prince Georges County: Suitland Bog, in seepage bog, introduced by A. V. Smith, growing successfully and spreading, 5 Aug 1947, *Walker 4162* (US); Suitland, open gravelly seepage, 20 Jul 1958, *Sargent 7671* (FSU). The Walker collection was reported by Shinners (1962). The earlier presence of deliberately introduced plants in an adjacent county makes the Charles County record questionable as a natural occurrence—the population could have been derived from Suitland Bog propagules. However, unless additional information indicates otherwise, the Cedarville population should be considered native.

In West Virginia, *Drosera filiformis* was reported, apparently without voucher, from Cranesville Swamp in Preston County (Breiding 1983), growing with *D. intermedia*, also a state record. These populations are considered to be introduced. Indeed, neither species has been located in several searches of the area by B. McDonald of the West Virginia Natural Heritage Program (pers. comm.).

Radford et al. (1968) documented *Drosera filiformis* from three North Carolina counties (Bladen, Columbus, and Duplin). Recent documentation exists for three additional counties. Brunswick County: disturbed pocosin along NC 211, Kologiski and McDonald, sight record (North Carolina Natural Heritage Program 1995). Pender County: open ditches along railroad, just south of Helena along SR 1412, *Sieren 3463* (WNC). Sampson County: abundant locally along grassy margins of Cutgrass Bay, with *Drosera intermedia* Hayne and *Pluchea rosea* Godfrey, 8 Jul 1989, *Sorrie 4740 with Weakley and LeBlond* (GH). Currently, there are nine extant populations in five counties (North Carolina Natural Heritage Program 1995).

In the Canadian province of Nova Scotia, a remarkable disjunct population was discovered in 1977 by J. Dowhan in an ombrotrophic, raised bog east of Barrington, Shelburne County. To my knowledge, this record has never been reported in the literature. Dowhan found an "extremely localized population in Swaine's Road Bog . . . growing in wet mud-bottom depressions . . . with *Sphagnum tenellum, S. flavicomens, Vaccinium macrocarpon, Rhynchospora alba, Sarracenia purpurea* & *Gymnocolea inflata*"; *Dowhan s.n.* (CONN, DAO, GH). In September of 1990 I visited a nearby bog, where numerous *Drosera filiformis* were growing with *D. intermedia* Hayne, *D. rotundifolia* L., *Ledum groenlandicum* Oeder, *Ilex glabra* (L.) Gray, *Schizaea pusilla* Pursh, and *Calamagrostis pickeringii* Gray; *Sorrie 5246* (NCU, pers. herb.). At that time, I was informed that thread-leaved sundew occurred at yet a third bog in the vicinity. All three bogs occur within two kilometers of the sea.

An even more remarkable disjunction occurs in the panhandle of Florida, discovered by R. Kral and R. K. Godfrey. There, at least eight populations are known from peaty sand shores of limesink ponds and one pond-like cypress bayhead. Dozens of other limesink ponds dot the landscape in the vicinity and more populations of *Drosera filiformis* are likely to be found. L. C. Anderson reported three collections from Washington County (Anderson 1991); otherwise, the presence of *D. filiformis* in Florida has not been documented in the literature. Bay County: sandy shores of Merial Lake north of Panama City by Florida rte. 77, 15 Jul 1970, *Kral 39938* (VDB); wet sandy shores of Merial Lake, north of Vicksburg, 10 Oct 1974, *Godfrey 73947* (FSU, VDB); exposed peaty-sandy shores of cypress head, 0.5 mi. south of jct. Florida routes 20 and 77, north of Vicksburg, 18 Sep 1982, *Godfrey 80000* (FSU); sandhills doline [= limesink or sinkhole pond] just south of Florida rte. 20, 3.7 mi. east of Crystal Lake and Florida rte. 77, 22 Jul 1991, *Kral 79463* (VDB). Washington County: limesink pond 0.7 mi. east of rte. 77, north side of Greenhead Road, 11 May 1989, *Bridges and Orzell 9785* (NCU); seepy margins of small pond in deep bowl northwest of Long Lake, south side of Greenhead Road, 2 Aug 1996, *Sorrie 8955* (GA, GH, NCU).

Wood (1960) questions the occurrence of *Drosera filiformis* in South Carolina and Georgia. I have found neither specimens nor documentation to support its occurrence there, and the state Natural Heritage Programs know of no verified record (B. Pittman and T. Patrick, pers. comm.).

Distribution—*Drosera tracyi*. In marked contrast, *Drosera* *tracyi* occurs exclusively on the Gulf Coastal Plain, from southwestern Georgia to southeastern Louisiana. The distribution of *D. tracyi* is continuous, without any disjunct populations (Figure 1).

Drosera tracyi has been well documented from Georgia, Florida, Alabama, and Mississippi, with representative specimens in regional and national herbaria. None of the Natural Heritage Programs in those states lists it as rare, except Georgia where it appears to be declining (T. Patrick, pers. comm.). Louisiana records, however, are not so well known. Riddell (1852) apparently was the first to report it from the state (as *D. filiformis*), but he gives no specific locality and there has been no voucher specimen located (MacRoberts 1989). Murry and Urbatsch (1979) cite a specimen collected in 1907, labeled "Plants of Louisiana, Wet pine barrens," *Cocks s.n.* (NO), but with no parish indicated. Fernald's generalized map (1931) shows *D. tracyi* in St. Tammany and Washington Parishes, but it is undocumented by specimens or verified sight records. On phytogeographical grounds, it is likely that Cocks secured his plants in southeastern Louisiana, for those parishes represent the western range limit for numerous species that inhabit the Gulf Coastal Plain. My own research (unpublished) on Gulf Coastal Plain endemics indicates that 160 species and varieties reach their western boundary in southeastern Louisiana.

Fernald (1950), Small (1933), and Wynne (1944) all state that *Drosera tracyi* occurs in South Carolina. Wood (1960) merely says that it has been reported from there, and Shinners (1962) likewise was unable to locate a specimen to verify the report. I, too, have failed to find any evidence of its occurrence in South Carolina. The state Natural Heritage Program knows of no verified record (B. Pittman, pers. comm.).

Drosera filiformis and *D. tracyi* occupy very distinct ranges. The former is nearly restricted to the Atlantic Coastal Plain; the latter is restricted to the Gulf Coastal Plain. Except for one limited area of sympatry in Bay and Washington Counties, Florida, the ranges of the two species are separated by a 550 km gap. In Washington County, Florida, Anderson (1991) reported finding one location where the two are actually syntopic (occurring together at a specific site).

DISCUSSION

Preparation and examination of accurate range maps can lead to the discovery of important or unusual phytogeographic patterns. By utilizing the formidable resources of the Gray Herbarium and of its library, Fernald (e.g., 1918, 1931) was able to prepare hundreds of maps that accompany his papers. These range maps were the basis for 1) establishing new regional, state, or county records, and 2) understanding the various patterns of distribution that plants exhibit. Similarly, James (1961), in his landmark paper on the endemic taxa of Florida, and Fryxell (1967), Reznicek (1994), and Wood (1972) in their papers on disjunctions, relied heavily on carefully prepared range maps. However, Fryxell stated this caution: "Yet the simple facts of distribution themselves rarely provide the basis for unequivocal interpretations. It is necessary to know . . . life form, ecological amplitude, mode of reproduction, capacity for dissemination of propagules, and cytological stability . . . before interpretations of their geographical distributions can take on solid meaning." In the previous section of this paper, I have presented data on distribution, morphology, ecology, and phenology of *Drosera filiformis* and *D. tracyi*. These data form the basis for decisions regarding taxonomic status. I believe that the data support treatment of the two as distinct species. The data also confirm the disjunct nature of the distribution of *D. filiformis* and the unbroken distribution of *D. tracyi*. In the remainder of the discussion section, I will attempt to interpret these distribution patterns in light of the historical geological context.

Forty-five years ago, Duncan (1953) questioned the availability of enough specimens to prepare adequate modern floras in the southeastern states. Perhaps as a result of this region-wide lack of distributional data, relatively few papers on the phytogeography of the Gulf and southern Atlantic Coastal Plains have been published. Since 1953, however, collections in southern herbaria have increased significantly. Floras and/or atlases are now available or are being produced in nearly every state from Virginia to Florida, Texas, and Arkansas. Gaps in our knowledge of taxonomy and distribution are rapidly becoming smaller. It seems that the time is ripe for comprehensive discussions of the phytogeography of this interesting and species-rich floristic region.

Species with similar ranges. Two other species pairs, plus a fifth species, occupy ranges that are very similar to the combined range of *Drosera filiformis* and *D. tracyi*. These species are *Coreopsis rosea* Nutt. and *C. nudata* Nutt., *Sabatia kennedyana*

Fern. and *S. foliosa* Fern., and *Lophiola aurea* Ker-Gawler. Each species pair, plus *Lophiola*, has a Gulf Coast component that is continuously distributed, and an Atlantic Coast component that has a highly disjunct distribution. Remarkably, all of the Atlantic components reach southwestern Nova Scotia, a region whose coastal plain affinities have been well documented (Roland and Smith 1969; Wisheu and Keddy 1989). Also remarkable is the fact that three of the Gulf Coast components (*C. nudata, D. tracyi*, and *L. aurea*) reach their western range limit within a few miles of each other in southeastern Louisiana. None of the seven species extends into peninsular Florida.

Sabatia kennedyana occurs disjunctly from Nova Scotia to South Carolina (Figure 2), paralleling the distribution of *Drosera filiformis*. However, *S. kennedyana* does not occur in New York, New Jersey, or Florida (Wilbur 1955). Like *D. filiformis*, it inhabits primarily sandy to boggy freshwater pond shores, where the two species often co-occur. In the Carolinas, *S. kennedyana* occurs on sandy drawdown shores of the Waccamaw River, a unique ecosystem which supports a number of "pond shore" species.

A second species of *Sabatia, S. foliosa*, occupies a more-or-less continuous distribution on the Gulf and southern Atlantic Coastal Plains (Figure 2). *Sabatia foliosa* occurs primarily in small, graminoid-shrub openings along blackwater streams (watercourses originating in the coastal plain, noted for their dark tannin-rich water), but also in pond cypress-black gum headwaters, and, in Louisiana and Texas, in marsh-like, periodically inundated depressions in pine savannas.

In the genus *Coreopsis*, two related species have distributions parallel to the two *Drosera*. *Coreopsis rosea* occurs disjunctly along the Atlantic Coastal Plain from Nova Scotia to southeastern Georgia. Over most of this range, *C. rosea* inhabits exposed shores of freshwater ponds, often in the company of *Sabatia kennedyana* and *D. filiformis*. In South Carolina, it inhabits sinkhole ponds, ponds in Carolina bays, and sandy drawdown shores of the Waccamaw River. The sole Georgia specimen (*Leavenworth s.n.*, PH) is presumably from a Carolina bay. Thus, the habitats of *C. rosea* are the same as, or analagous to, those of *D. filiformis*.

The second species of this pair, *Coreopsis nudata*, ranges from southeastern Georgia to southeastern Louisiana (Figure 3). It inhabits periodically inundated depressions which usually support

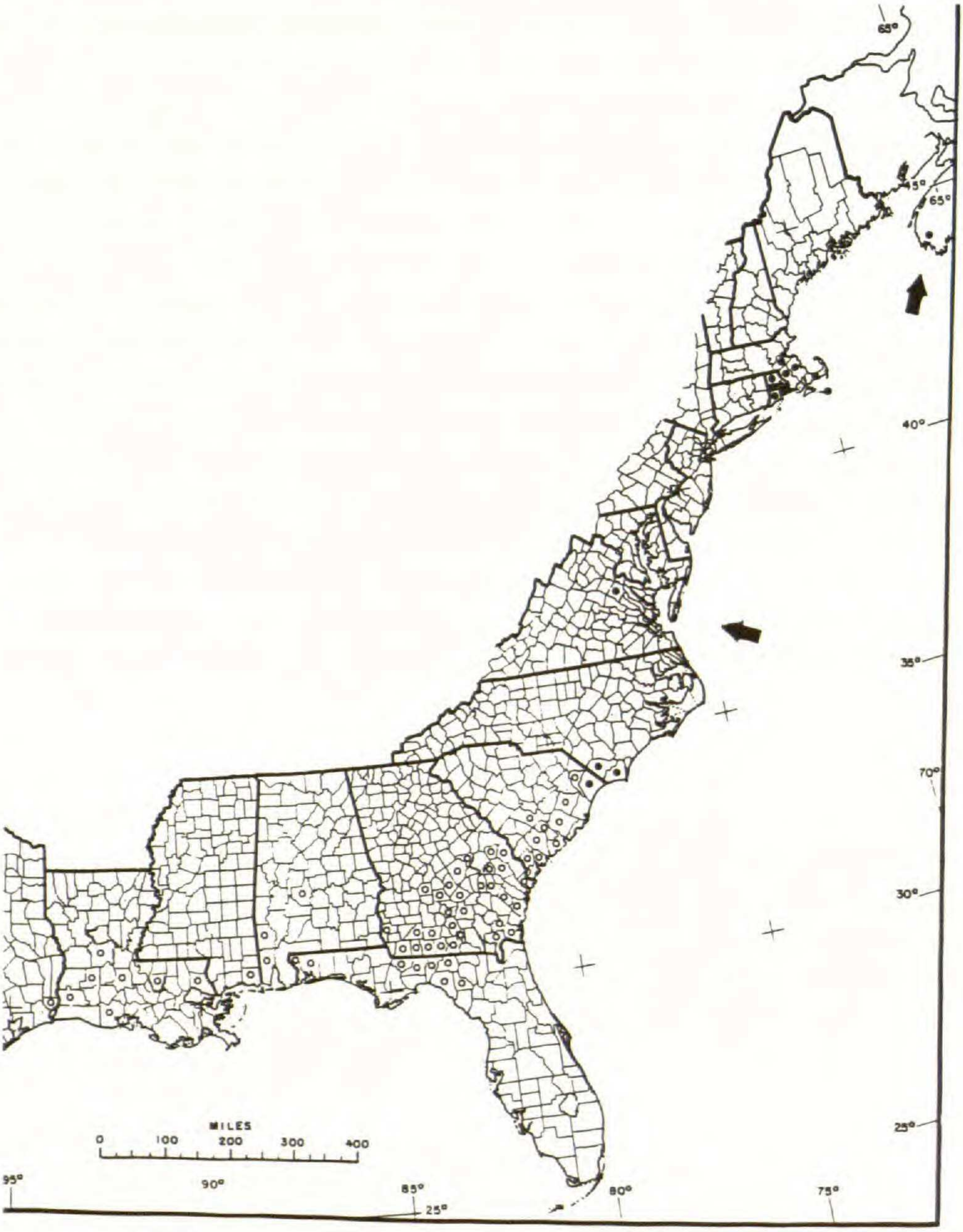

Figure 2. Distribution of *Sabatia kennedyana* and *S. foliosa*. Solid dots = *S. kennedyana* (Nova Scotia to South Carolina); open circles = *S. foliosa* (South Carolina to Texas).

pond cypress (*Taxodium ascendens* Brongn.), black gum (*Nyssa biflora* Walter), woody St. Johnsworts (*Hypericum fasciculatum* Lam., *H. chapmanii* P. Adams, and others), *Sabatia bartramii* Wilbur, and various graminoids, especially *Rhynchospora careyana* Fern. Variations of this habitat type are called cypress ponds,

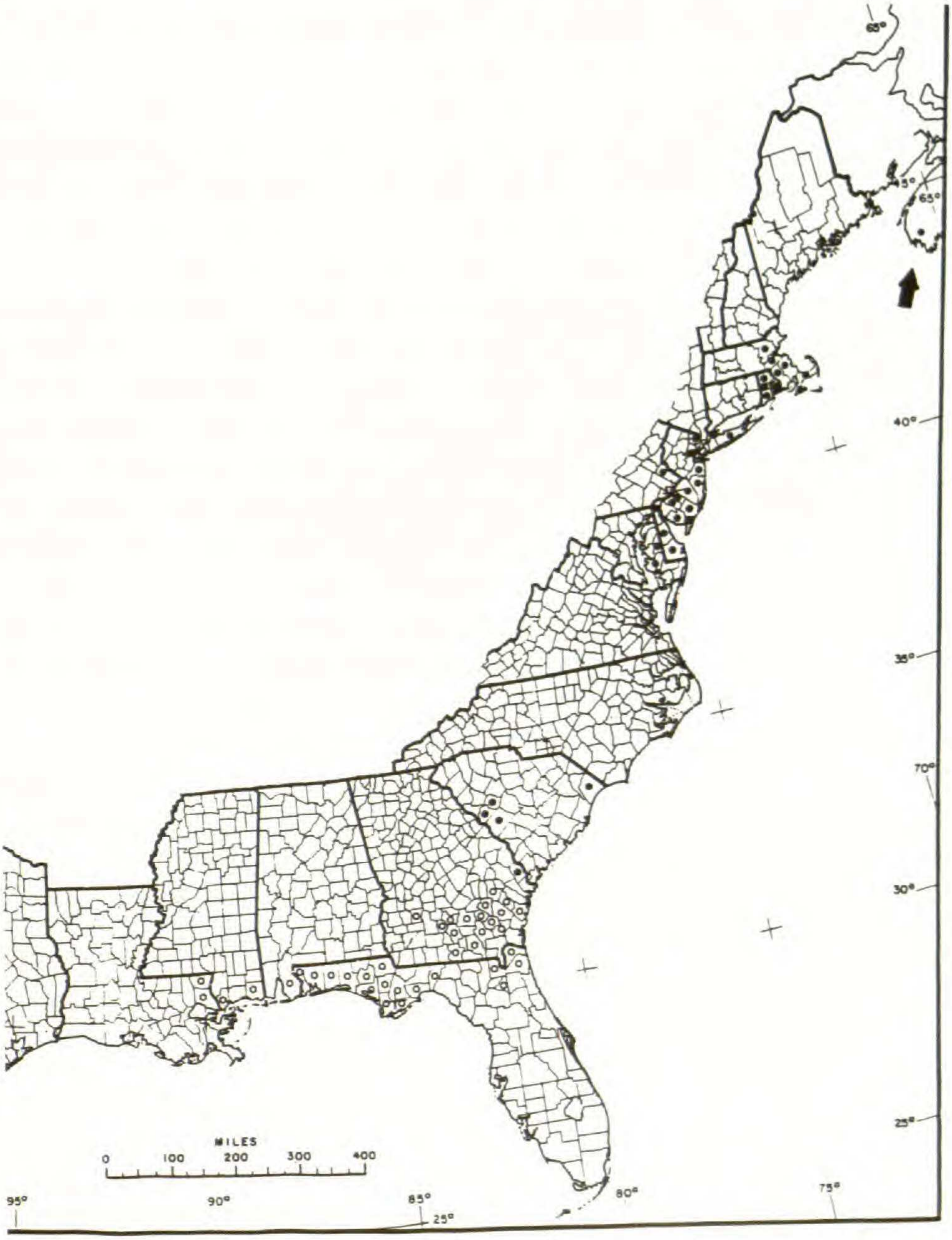

Figure 3. Distribution of *Coreopsis rosea* and *C. nudata*. Solid dots = *C. rosea* (Nova Scotia to Georgia); open circles = *C. nudata* (Georgia to Louisiana).

cypress domes, cypress stringers, and *Hypericum* ponds. Botanists often collect *C. nudata* from roadside ditches, a result of highway departments' proclivities to bisect its natural habitats. *Coreopsis nudata* does not, so far as I know, occur syntopically with *Drosera tracyi*. *Coreopsis nudata* and *C. rosea* are the only two pinkflowered species in the genus in North America, and although they are placed in the same section (Smith 1976), they possess marked differences in leaf arrangement, leaf morphology, and achene morphology. If they are to be viewed as a species pair, then it is reasonable to assume that they diverged (from a common precursor) longer ago than the split of the two *Drosera*, which have not diverged very much morphologically.

Lophiola aurea has a distribution that closely matches the combined ranges of *Drosera filiformis* and *D. tracyi.* It is primarily a Gulf Coastal Plain species, with disjunct occurrences scattered along the Atlantic Coastal Plain (Figure 4). Unlike *D. filiformis*, *Lophiola* is absent from Long Island, New York, and southeastern New England. One possible reason for this is its preference for seepage bogs and wet savannas, habitats essentially unavailable in those northern areas. In pitcher plant bogs of the Gulf Coastal Plain, *Lophiola* is abundant and is a common associate of *D. tracyi*. In North Carolina, it inhabits seasonally inundated depressions in wet, pine-wiregrass savannas and similar depressions in old river terraces. In New Jersey it occurs in streamside seepage bogs, locally called "savannas." In Nova Scotia, it occurs primarily in peaty, graminoid-dominated, riverside "savannas" (Roland and Smith 1969), but also on the shores of two lakes. Ecologically, the New Jersey and Nova Scotia "savannas" are actually acidic, poor fens, analogs of the Gulf Coastal Plain "bogs."

Fernald (1922, 1950) treated Nova Scotia plants as *Lophiola septentrionalis* Fern., but subsequent authors have not recognized them as distinct (Gleason 1952; Gleason and Cronquist 1991; Roland and Smith 1969; Scoggan 1978; Small 1933). Robertson (1976) compared Nova Scotia specimens with living plants in North Carolina and suggested that some of the variation that Fernald described may be due to ecological factors. My own observations from throughout the range lend support—rhizome thickness, corymb width, pedicel length, indument density, and capsule color (distinguishing characters used by Fernald) vary considerably. Robertson added that widely disjunct populations in a species would be expected to differ from each other. Until a detailed taxonomic study is completed, it seems best to regard *L. septentrionalis* as a synonym of *L. aurea*.

Phytogeographic patterns. The pattern displayed by the

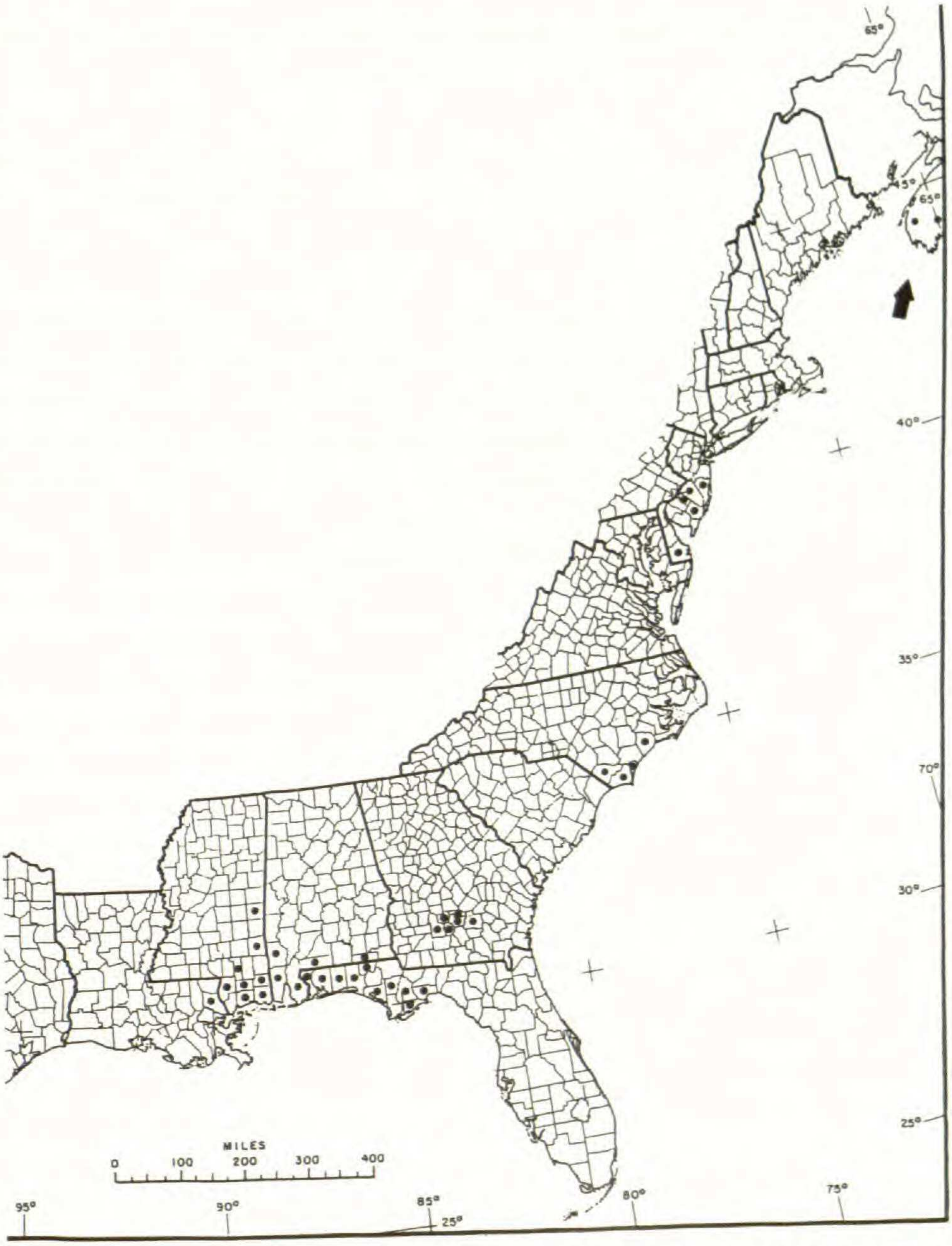

Figure 4. Distribution of *Lophiola aurea* (Nova Scotia to Louisiana).

Gulf Coast representatives of the species pairs is a common one—there are 160 taxa (species and varieties) of vascular plants which are endemic to the East Gulf Coastal Plain, a narrow band extending from southwestern Georgia through panhandle Florida to southeastern Louisiana (my own unpublished data). Another 57 taxa occupy a similar range, but extend westward across the Mississippi River to western Louisiana and/or eastern Texas. Four genera (*Brintonia* in the Asteraceae, *Harperocallis* in the Liliaceae, *Macranthera* in the Scrophulariaceae, and *Stachydeoma* in the Lamiaceae) are endemic to the East Gulf Coastal Plain, and a fifth (*Stokesia* in the Asteraceae) is nearly so. All five genera are monotypic; they may represent relicts that were more wide-ranging in the past. Clearly, Gulf Coastal Plain endemics represent a large and important component of the coastal plain flora as a whole. Ninety years ago, Harper (1907) noted that this region was a center of distribution for coastal plain plants, but no modern synthesis has been written, in part because this region remains seriously undercollected. Papers discussing phytogeographic patterns are scarce (but see Bridges and Orzell 1989a, b; Orzell and Bridges 1987).

The pattern displayed by the Atlantic Coast representatives of the species pairs is apparently unique. Many coastal plain plant taxa show minor disjunctions, but only *Coreopsis rosea*, *Drosera filiformis*, *Sabatia kennedyana*, and *Lophiola aurea* show three major disjunctions along the length of the Atlantic Coastal Plain. In the zoological realm, the distribution of the pine barrens tree frog (*Hyla andersonii*) shows two major disjunctions: from the Florida panhandle and adjacent Alabama to the Carolinas to southern New Jersey. This amphibian inhabits many of the same Gulf Coast seepage bogs as do *L. aurea* and *D. tracyi*, as well as similar bogs in New Jersey, where *D. filiformis* occurs.

I postulate that the four Atlantic disjuncts (or their progenitors) reacted very similarly to the ecological and climatic forces of the Pleistocene and that they migrated from the Gulf region out along the exposed Atlantic continental shelf as favorable conditions and habitats became available. Quaternary vegetation maps prepared by Delcourt and Delcourt (1981), based on pollen cores throughout eastern North America, suggest that the Gulf and southern Atlantic Coastal Plains supported "Oak-Hickory-Southern Pine Forest" continuously from 40,000 to 10,000 yr B. P. By 5000 yr B. P., the modern "Southern Pine Forest" had become dominant. Moreover, ". . .the Gulf Coastal Plain has remained relatively unaffected by substantial temperate changes, even during the peak in Wisconsinan continental glaciation 18,000 years ago" (Delcourt and Delcourt 1981). It seems likely that the Gulf and southern Atlantic Coastal Plains served as refugia for plants during much of the Pleistocene. Furthermore, the large numbers of endemic species (160) and genera (5) which now inhabit the East

Gulf Coastal Plain strongly suggest that the processes of speciation continued uninterruptedly during that period. In the case of *Drosera*, *Coreopsis*, *Sabatia*, and *Lophiola*, the process of migrating to the Atlantic Coastal Plain may have involved several glacial cycles, as populations became established and then extirpated. Although the taxa occupied similar habitats, each moved independently according to its dispersal capabilities. Eventually, isolation of the plant populations on the two coastal plains became great enough to allow for speciation, except in *Lophiola*.

Once populations of *Drosera*, *Coreopsis*, *Sabatia*, and *Lophiola* became established on the southern Atlantic Coastal Plain, it remained for them to move northward. Fernald (1931), Roland and Smith (1969), and others have postulated that during the last glaciation, coastal plain plants survived on the exposed continental shelf of the Atlantic Coast. The authors postulate that plants occupied continuous ranges along a broad latitudinal band. However, pollen core data (Delcourt and Delcourt 1981) suggest that during most of the past 40,000 years, the coastal plain from North Carolina northward was dominated by forests of jack pine and spruce. Under such cold climatic conditions, southern taxa were highly unlikely to survive north of the Carolinas, even in near-coastal habitats. Available evidence indicates that coastal plain plants did not occupy middle and northern Atlantic regions until after major climatic amelioration and retreat of the Wisconsin glaciers around 12,500 years ago.

Once climatic warming took place, coastal plain plants had two avenues of northward migration: incrementally by dispersing through continuous vegetation types or disjunctly via discontinuous types. Examples of species which probably migrated incrementally are *Dichanthelium scoparium* (Lam.) Gould, *Euthamia tenuifolia* (Pursh) Nutt., *Gaylussacia frondosa* (L.) Torrey & Gray, *Lyonia mariana* (L.) D. Don, and *Woodwardia virginica* (L.) Smith. These species are widespread on the coastal plain today and occupy habitats that are relatively continuous on the landscape. There is no compelling reason to doubt that such habitats were also widespread during the late Pleistocene and Holocene. Movement of propagules from one suitable habitat to another involved short-distance dispersal.

In contrast, the Atlantic species of *Coreopsis*, *Drosera*, *Lophiola*, and *Sabatia* apparently migrated disjunctly, if we assume that their habitats (ponds or poor fens) occurred discontinuously on the landscape, as they do today. As suggested by Jackson and Singer (1997) and Reznicek (1994), dispersal events may have occurred between wetlands 10–100 km apart. Although longer distances may have been successfully bridged, such dispersal events were presumably rare and are not necessary to explain the current distributions of the Atlantic disjuncts. By 10,000 yr B. P., the climate had ameliorated significantly, allowing southern plants to move northward as suitable habitats became available; about this time peat bogs developed in what is now the New Jersey Pine Barrens (Buell 1970). By 5000 yr B. P., sea level had returned to its modern position and Oak-Hickory-Southern Pine communities had reached Long Island, New York (Delcourt and Delcourt 1981). After 5000 yr B. P., there was no way for plants to reach Nova Scotia except via long-distance dispersal. Thus, plants had roughly 5000 years in which to migrate from the southern Atlantic Coastal Plain to New Jersey, southern New England, and Nova Scotia. Assuming only modest dispersal distances (less than 100 km), and allowing for local extirpations, there was ample time for plants to reach these northern areas (distance from Cape Hatteras, North Carolina, to Yarmouth, Nova Scotia is 1290 km). At the end of that period, major portions of the Atlantic Coastal Plain were inundated—Albemarle Sound, Pamlico Sound, Chesapeake Bay, Delaware Bay, Long Island Sound, Georges Bank, Bay of Fundy—and no longer available to plants. Moreover, the extirpation in those regions of coastal plain wetland plants contributed significantly to creating disjunctions on their ranges. However, it is unlikely that the extreme disjunction shown by *Coreopsis*, *Drosera*, *Lophiola*, and *Sabatia* can be explained merely by sea level rise—one of the major disjunctions occurs in the Georgia-South Carolina region, which was apparently little affected by inundation.

Dispersal of propagules from one wetland to another may happen irregularly or frequently, but successful colonization (establishment of a stable breeding population) depends on several factors. First, a species's optimal plant community may occupy only a fraction of the available wetlands, given natural variations in hydroperiod, soil nutrients, soil texture, and microclimate. Second, movement of propagules does not occur uniformly, but irregularly by mammals (including humans), waterfowl, and probably also by severe weather events. Third, successful colonization may not occur until after repeated dispersal events, as previous populations die out. Fourth, the number of wetlands decreased sharply during climatic warming as rising sea level inundated the continental shelf, especially in the mid- to north Atlantic region. As a consequence, propagules were less likely to reach suitable habitats, which in turn created disjunctions between plant populations. After the middle Holocene, northward colonization of coastal plain wetlands would have required long-distance dispersal. In my view, this is an unlikely scenario for the four species of *Coreopsis*, *Drosera*, *Lophiola*, and *Sabatia*. That all four could have such a similar pattern of disjunctions, due solely to random long-distance dispersal, is extremely unlikely. Rather, the biogeographical pattern exhibited by *C. rosea*, *D. filiformis*, *L. aurea*, and *S. kennedyana* is the product of 1) short-distance dispersal events carried out over a relatively long period of time (late Pleistocene-early Holocene); 2) different dispersal and establishment capabilities of each species; and 3) loss of intervening populations due to inundation, senescence, or other means.

The above hypothesis is speculative, but may be strengthened by additional sampling of pollen cores at sites along the length of the Atlantic Coastal Plain. Unfortunately, a critical area for such study lies in the now-inundated portion of the continental shelf. Although a considerable number of cores have been taken from the inner shelf (Emery et al. 1967; Field et al. 1979; Livingstone 1964), the relatively meager diversity of pollen recovered has not led to an increased understanding of population ecology during the Pleistocene. A major problem to overcome is the identification of pollen samples down to the species level.

In summary, available evidence suggests that populations of *Drosera*, *Sabatia*, *Coreopsis*, and *Lophiola* were neither abundant nor continuous on the continental shelf during the late Pleistocene. To account for past and present distributions, it is not necessary to assume that these taxa ranged continuously along the length of the coastal plain, nor that they migrated via long-distance dispersal events. Modern distributions of Atlantic Coastal Plain plants, including species with broad disjunctions, can be accounted for by normal dispersal and establishment during the past 15,000 years.

ACKNOWLEDGMENTS. Rick Enser, Les Mehrhoff, David Snyder, and Robert Zaremba provided information on the ecology and history of *Drosera filiformis* in Rhode Island, Connecticut, New Jersey, and New York, respectively. Joseph Dowhan kindly provided me with data on his discovery of *Drosera filiformis* in Nova Scotia. Richard LeBlond and an anonymous reviewer made substantial improvements to previous drafts. I am grateful to the curators and managers of the following herbaria for access to their collections: A, CONN, DUKE, FLAS, FSU, GA, GH, IBE, LSU, MASS, MISSA, NCSC, NEBC, NLU, NMMA, NCU, PH, USA, USCH, VDB, and VSC.

LITERATURE CITED

ANDERSON, L. C. 1991. Noteworthy plants from north Florida. V. Sida 14: 467–474.

BAILEY, L. H. 1914. The Standard Cyclopedia of Horticulture. Macmillan, New York.

BREIDING, M. 1983. Two *Drosera* (sundew) species new to West Virginia. Castanea 48: 55.

BRIDGES, E. L. AND S. L. ORZELL. 1989a. Additions and noteworthy vascular plant collections from Texas and Louisiana, with historical, ecological, and geographical notes. Phytologia 66: 12–69.

——— AND ———. 1989b. Longleaf pine communities of the West Gulf Coastal Plain. Nat. Areas J. 9: 246–263.

BUELL, M. F. 1970. Time of origin of New Jersey Pine Barrens bogs. Bull. Torrey Bot. Club 97: 105–108.

CLEWELL, A. F. 1985. Guide to the vascular plants of the Florida Panhandle. University Presses of Florida, Tallahassee, FL.

DELCOURT, P. A. AND H. R. DELCOURT. 1981. Vegetation maps for eastern North America: 40,000 yr B.P. to the present, pp. 123–165. *In:* R. C. Romans, ed., Geobotany II. Plenum Press, New York.

DUNCAN, W. H. 1953. Taxonomic collections of vascular plants in the southeastern states—their abundance and relation to production of floras. Rhodora 55: 353–358.

EMERY, K. O., R. L. WIGLEY, A. S. BARTLETT, M. RUBIN, AND E. S. BARGHOORN. 1967. Freshwater peat on the continental shelf. Science 158: 1301–1307.

FERNALD, M. L. 1918. The geographic affinities of the vascular floras of New England, the Maritime Provinces, and Newfoundland. Amer. J. Bot. 5: 219–236.

———. 1922. Notes on the flora of Nova Scotia. Rhodora 24: 167.

———. 1931. Specific segregates and identities in some floras of eastern North America and the Old World. Rhodora 33: 53–55.

———. 1950. Gray's Manual of Botany, 8th ed. American Book Co., Boston, MA.

FIELD, M. E., E. P. MEISBURGER, E. A. STANLEY, AND S. J. WILLIAMS. 1979. Upper Quaternary peat deposits on the Atlantic inner shelf of the United States. Bull. Geol. Soc. Amer. 90: 618–628.

FOLKERTS, G. W. 1991. A preliminary classification of pitcher plant habitats in the southeastern United States. J. Alabama Acad. Sci. 62: 199–225.

FRYXELL, P. A. 1967. The interpretation of disjunct distributions. Taxon 16: 316–324.

GLEASON, H. A. 1952. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. The New York Botanical Garden, Bronx, NY.

——— AND A. CRONQUIST. 1991. Manual of Vascular Plants of Northeastern United States and Adjacent Canada, 2nd ed. The New York Botanical Garden, Bronx, NY.

GODFREY, R. K. AND J. W. WOOTEN. 1981. Aquatic and Wetland Plants of Southeastern United States. Vol. 2, Dicotyledons. Univ. Georgia Press, Athens, GA.

HARPER, R. M. 1907. Centers of distribution of coastal plain plants. Science, New Series, 25: 539–541.

———. 1914. A superficial study of the pine-barren vegetation of Mississippi. Bull. Torrey Bot. Club 41: 551–567.

JACKSON, S. T. AND D. K. SINGER. 1997. Climate change and the development of coastal plain disjunctions in the central Great Lakes region. Rhodora 99: 101–117.

JAMES, C. W. 1961. Endemism in Florida. Brittonia 13: 225–244.

JONES, S. B., JR. AND N. C. COILE. 1988. The Distribution of the Vascular Flora of Georgia. Dept. of Botany, University of Georgia, Athens, GA.

KARTESZ, J. T. 1994. A Synonymized Checklist of the Vascular Flora of the United States, Canada, and Greenland, 2nd ed. 2 vols. Timber Press, Portland, OR.

LEE, D. S. AND A. W. NORDEN. 1972. The thread-leaf sundew, *Drosera filiformis* on the coastal plain of Maryland. Castanea 37: 302.

LINK, W. R., JR. 1965. *Drosera filiformis* in Connecticut. Rhodora 67: 273.

LIVINGSTONE, D. A. 1964. The pollen flora of submarine sediments from Nantucket Shoals. Amer. J. Sci. 262: 479–487.

LOWE, E. N. 1921. Plants of Mississippi. Miss. State Geol. Survey Bull. 17. Jackson, MS.

MACROBERTS, D. T. 1989. A Documented Checklist and Atlas of the Vascular Flora of Louisiana. Dicotyledoneae: Acanthaceae to Fabaceae. Bull. Mus. Life Sci. Louisiana State Univ., No. 8. Shreveport, LA.

MURRY, R. E., JR. AND L. E. URBATSCH. 1979. Preliminary reports on the flora of Louisiana. III. The families Droseraceae and Sarraceniaceae. Castanea 44: 24–27.

NORTH CAROLINA NATURAL HERITAGE PROGRAM. 1995. Database records for *Drosera filiformis*. North Carolina Natural Heritage Program, Division of Parks and Recreation, Raleigh, NC.

ORZELL, S. L. AND E. L. BRIDGES. 1987. Further additions and noteworthy collections in the flora of Arkansas, with historical, ecological, and phytogeographical notes. Phytologia 64: 81–144.

RADFORD, A. E., H. E. AHLES, AND C. R. BELL. 1968. Manual of the Vascular Flora of the Carolinas. Univ. North Carolina Press, Chapel Hill, NC.

RAFINESQUE-SCHMALTZ, C. S. 1808. Essential generic and specific characters of some new genuses and species of plants observed in the United States of America in 1803 and 1804. Medical Repository II, 5: 360.

REZNICEK, A. A. 1994. The disjunct coastal plain flora in the Great Lakes region. Biol. Conserv. 68: 203–215.

RIDDELL, J. L. 1852. Catalogus Florae Ludoviciana. New Orleans Med. Surg. J. 8: 734–754.

ROBERTSON, K. R. 1976. The genera of Haemodoraceae in the southeastern United States. J. Arnold Arb. 57: 205–216.

ROLAND, A. E. AND E. C. SMITH. 1969. The Flora of Nova Scotia. Nova Scotia Museum, Halifax, Nova Scotia. [Discussion of coastal plain species on pp. 302–307.]

SCHNELL, D. E. 1976. Carnivorous Plants of the United States and Canada. John F. Blair, Winston-Salem, NC.

SCOGGAN, H. J. 1978. The Flora of Canada. National Museums of Canada, Ottawa, Ontario.

SHINNERS, L. H. 1962. *Drosera* (DROSERACEAE) in the southeastern United States: An interim report. Sida 1: 53–59.

SMALL, J. K. 1933. Manual of the Southeastern Flora. Privately printed. Reprinted 1972 by Hafner Publishing Co., New York.

SMITH, E. B. 1976. A biosystematic survey of *Coreopsis* in eastern United States and Canada. Sida 6: 123–215.

TATNALL, R. R. 1946. Flora of Delaware and the Eastern Shore. Society of Natural History of Delaware, Wilmington, DE.

TUCKER, G. 1978. Notes on the flora of Rhode Island. Rhodora 80: 596–597.

WILBUR, R. L. 1955. A revision of the North American genus *Sabatia*. Rhodora 57: 1–33, 43–71, 78–104. [Subsection Dodecandrae on pp. 78–96.]

WILHELM, G. AND J. R. BURKHALTER. 1994. Vascular flora of the Pensacola Region. Checklist and field desiderata. Revised May 1994. Privately printed.

WISHEU, I. C. AND P. A. KEDDY. 1989. The conservation and management of a threatened coastal plain plant community in eastern North America (Nova Scotia, Canada). Biol. Conserv. 48: 229–238.

WOOD, C. E., JR. 1960. The genera of Sarraceniaceae and Droseraceae in the southeastern United States. J. Arnold Arbor. 41: 152–163.

———. 1972. Morphology and phytogeography: The classical approach to the study of disjunctions. Ann. Missouri Bot. Gard. 59: 107–124.

WYNNE, F. E. 1944. *Drosera* in eastern North America. Bull. Torrey Bot. Club 71: 166–174.